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The Innervation of the Integument of Chiroptera

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THE INNERVATION OF THE INTEGUMENT OF CHIROPTERA

BY

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I HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER MY SUPERVISION BY

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ENTITLED The Innervation of the Integument of Chiroptera

BE ACCEPTED AS FULFILLING THIS PART OF THE REQUIREMENTS FOR THE

DEGREE OF Doctor of Philosophy.

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INTRODUCTION.

The ease and precision with which blinded bats avoid obstacles while on the wing attracted the attention of eighteenth century investigators, who, at that early date, thought the wing membranes were sensitive to external stimuli. Cuvier, in 1796, set forth the theory that the patagium and ears were capable of perceiving air currents set up between the object and the approaching animal. Later, Schöbl (1871) described special sensory organs, "Terminalkörperchen", at the base of each hair. As both end-organ and hair were thought to be richly innervated, they were supposed to form the mechanism for the perception of obstacles. Recently, attempts have been made to explain this phenomenon by other means. Rollinat and Trouessart (1900) attributed this power to a sixth sense, that of direction; while Hahn (1908) was convinced that objects were perceived chiefly through sense organs located in the internal ear.

Responses of captive bats to tactile stimuli applied to various parts of their bodies and membranes are very vigorous. The lack of agreement among observers on the nature and location of the perceptive organs of bats, the extreme sensitiveness of the integument, and the possibilities of modern technique seemed to justify a further search for sensory structures in the skin of these animals. Furthermore, at the time this work was begun, no investigator had made an extensive study of the inner-

vation of the skin of bats since Schöbl published in 1871 his account of the terminal corpuscles in the flying membrane.

The work has been carried on during the last three years in the Zoological Laboratory of the University of Illinois under the direction of Professor Frederic W. Carpenter, to whom I am indebted not only for his personal interest in the progress of the work, but also for his constant advice and helpful criticisms.

PHYSIOLOGICAL AND ANATOMICAL EVIDENCE OF THE EXTREME SENSITIVENESS OF THE SKIN OF BATS.

The first investigation of the sensitiveness of the skin of bats, so far as the writer has been able to ascertain, was the well known experiment of Spallanzani in 1793. This investigator blinded bats, and observed that they avoided with accuracy not only large obstacles placed in their way, but even silken threads stretched in such a manner as to leave only sufficient space for the bats to pass between with their wings expanded.

In 1796 Cuvier called attention to the exquisite sense of touch in the membranous skin covering the wings and ears. Upon examination he found the wings to be supplied with an enormous number of nerves. He inferred that during flight the blinded bat, on approaching the object, sets up air currents, which, reacting on the sensitive patagium and ears, enable the animal to perceive and to avoid the obstacle.

Jurin, in 1798, performed experiments similar to those of Spallanzani. The blinded bats avoided the obstacles success-

fully, but were unable to do this when their organs of hearing were destroyed.

Leydig (1859), who was of the opinion that the nerves of the flying membrane were not more numerous than those of the ordinary skin, thought that Cuvier had mistaken the elastic bridges (Balken) for nerves.

Schöbl (1871) experimenting on a bat kept for a year in his living room confirmed Spallanzani's findings. This investigator made an extensive anatomical study of the flying membranes of Chiroptera. He found not only an abundance of nerves, but also an intricate network of nerve fibers and, at the bases of the hair follicles, numerous end-organs, "Terminalkörperchen", which in his opinion were closely allied to the touch organs (Tastkörperchen) of other mammals. In the same year Boll, working with Schöbl, confirmed the latter's findings.

Stieda (1872) seriously questioned Schöbl's results. He emphatically denied that Schöbl's "Terminalkörperchen" were found as a rule in all bats. Moreover, he treated these structures as hair growths (Haarkeime) and not as nerve organs.

During the same year, Veleeky repeated Schöbl's work, using the latter's method. This investigator also failed to find the so-called "Terminalkörperchen". Furthermore, he used another method (gold) and still failed to find the structures in question at the bases of the hairs.

Jobert (1872) was of the opinion that the touch apparatus of bats was located in the flying membrane, and that these touch organs, viz., the richly innervated hairs, played an im-

portant part in determining the habits of the animals. According to this investigator each movement of the hair was transmitted to the nerve ring which surrounded it. In this way nervous impulses were originated, and objects were perceived and avoided.

In 1873, Redtel repeated Spallanzani's experiments. Threads, etc., were stretched across a small room, in which a normal bat was liberated. The animal flew with great speed. While it seltouched the thread with its wings, it never touched the threads with its head. The bat was then blinded and set free again. Its flight was now somewhat less accurate, but it avoided the threads just as it did before. He then clipped the vibrissae from the face, but the flight of the bat was not affected. From the abundance of nerves found by Schöbl in the flying membrane, and from his own experiments, Redtel inferred that it was possible for bats to perceive the slightest change of air pressure upon the wings. He explained the few failures to avoid the obstacles in the following way: Ordinarily, the flying bat begins to prepare itself for turning away from the obstacle when it is approximately at the distance of a meter from it, but when flying rapidly there is not always sufficient time for the avoiding movement to take place.

Arnstein (1876) investigated the innervation of the flying membrane. He found nerve trunks, closely interwoven nerve networks, free thread-like fibers extending up from the networks into the epidermis, and perceptive corpuscles.

Flower and Lydekker (1891) advanced the view that it is the

delicate sense of touch which enables bats deprived of sight, hearing and smell to avoid obstacles. They were of the opinion that tactile organs exist in connection with the vibrissae of the face, in the ear conchs, and in the wing membranes.

In 1907, Schumacher mentioned the presence of a large number of layer-like corpuscles (Lamellenkörperchen) among the phalanges of bats.

Hahn (1908) carried out extensive experiments in which he caused a large number of mutilated bats to make a given number of flights in an enclosure through which numerous wires had been stretched. His experiments showed that the destruction of the sense of sight does not seriously impair their ability to perceive objects, nor does the loss of external ears and tragi. As the hairs of the body and flying membrane were supposed to have a sensory function, Hahn coated them with thick vaseline, which caused them to adhere to one another, and, hence, to be less sensitive to slight stimulation. The results of this experiment are given thus in Hahn's paper: "Five examples of Myotis lucifugus with the hair so coated struck 34.6 per cent. of the chances. Five M. sublatus struck 39.6 per cent. of trials with hair covered, and 24.4 per cent. when normal. For five Pipistrellus subflavus the proportions were 32.4 per cent. and 25.2 per cent." Thus it is seen that in this experiment the average number of hits of all the bats whose hair was covered, was approximately 10 per cent. greater than that of normal bats. From this and other experiments Hahn concluded that the organs of touch located in the skin and probably associated with the hairs are of value in enabling the animals to avoid objects,

though of less value than the auditory organs. He also states that the tactile sense located in the vibrissae and in the lips is very delicate, and doubtless aids the animal in locating its food.

MATERIAL AND METHODS.

The material for this investigation consisted of forty-one bats of which thirty-one were cave bats (Myotis lucifugus) from Indiana. The remainder, the common red bats (Myotis sublatus), were taken the vicinity of Urbana, Illinois.

As the greater part of the material was prepared by an intra vitam methylene blue method, the latter is here given in detail.

Etherize or chloroform the animal until it is deeply narcotized, but not quite dead. To secure free circulation (free circulation) of the staining fluid through the wing and interfemoral membranes it is best not to fasten the bat to the injection board. Open the thoracic and pericardial cavities and make an incision in the left ventricle (being careful not to cut into the right ventricle). After allowing the blood to flow out through the cut, swab out the thorax with a bit of absorbent cotton, and place a loose ligature around the base of the aorta. For injecting, a syringe with a detachable rubber tube and a small glass canula is very satisfactory. Insert the canula through the left ventricle into the base of the aorta, and tie it with the ligature. For an overflow make a small opening in the right auricle. Inject Ringer's solution warmed to body

temperature into the aorta until most of the blood is washed out, i.e., until the clear solution comes out at the right auricle. Inject a 1% solution of methylene blue in distilled water warmed to body temperature into the blood system until the integument looks blue. Clamp the right auricle. With the blood vessels still full of the staining fluid leave the animal freely exposed to the air three-fourths of an hour for oxidation. If, at the close of the injection, the integument is not a deep blue, inject more of the methylene blue solution after a period of ten minutes. After allowing ample time for oxidation, wash the methylene blue out of the vessels with Ringer's solution (warmed to body temperature) and remove the apparatus. Small pieces of integument may now be taken off, exposed to the air for a few minutes, and then placed in a cold 8% solution of ammonium molybdate in distilled water. (Must be made fresh). Leave the pieces of skin in the ammonium molybdate (fixing) solution at least twelve hours. Wash in running water three hours. For this purpose small porcelain sieves with minute perforations and cork stoppers are very serviceable. Pass the tissues through the alcohols, 70%, 95%, 100%, leaving them for a period of three hours in each. To prevent the methylene blue from dissolving out, the tissues should be kept cold (5 to 10° C) while they are in the alcohols. Clear in xylol (3to5 hours). A mixture of two parts hard paraffine to one part soft is best suited for imbedding the flying membrane, while for the skin of the body which is more cornified, hard paraffine is preferable. Sections cut 20 micra are thick enough to enable one to follow

nerve fibers some distance, and sufficiently thin to admit ample light. Mount in balsam.

The following short method of affixing the sections to the slide may be used to good advantage. Place on a clean glass slide a small drop of fixative prepared by mixing equal parts of oil-of-cloves and collodion. Rub until a thin coating is formed. Lay upon the slide the paraffine ribbons of thick (20 micra) sections, and flatten them out by pressing down with the tip of the finger. Place slide in xylol until paraffine is dissolved off and mount in balsam.

Other killing and fixing fluids used were corrosive sublimate and acetic acid, Zenker's fluid, ammoniacal alcohol (8 to 10 drops of aqua ammonia to 1000 cc. 95% alcohol) and 10% formol.

Besides methylene blue the following stains were used: silver nitrate (Cajal method for nerve fibrils), carmalum as a counter stain for methylene blue, Mallory's connective tissue stain, Heidenhain's iron haematoxylin, Delafield's haematoxylin and eosin, and Hanson's haematoxylin and orange G.

OBSERVATIONS AND DISCUSSION.

I.-General Structure of the Integument.

1. Integument of the Body.

The skin of the body of bats is covered with hair which, as Allen (1893) has found, varies in different regions in texture and amount. In general, the crown of the head, the neck,

the sides of the under surface of the body, the rump and the pubis have a thick pelage, while the distal portions of the ears, the soles of the feet, the mammae and external genitalia are almost naked. The snout is scantily clothed, but shows a limited number of vibrissae which arise from wart-like structures.

In different regions of the body the skin varies greatly in thickness. The integument of the face is the deepest. That of other parts of the body diminishes in depth gradually in the following order: palmar region, plantar region, rump, ventral thoracic region, crown, and dorsal thoracic region.

As a rule some difficulty is experienced in distinguishing all the layers commonly found in the human integument. In the epidermis the Malpighian or deeper stratum can be readily made out. Its deepest layer is made up of subcolumnar cells. The intermediate layer of polygonal cells is for the most part absent, though in places (e.g., the face) it appears as a single sheet of isolated, more or less flattened cells, whose nuclei are somewhat reduced in size (Fig.1). Numerous pigment granules are present in this layer (Fig.2,pg).

The stratum corneum is thickest in the palmar and plantar regions. It is made up of several layers of cornified epithelium, the outer ones of which are usually in the form of loose scales. The deeper layers are more compact, and appear to consist of flat, enucleate cells. In certain regions of the body (lining of the mouth, lumbar region) these layers resemble to some extent the stratum lucidum of the human skin, but the presence of this stratum can be made out definitely only in the palmar and plantar regions,(Fig.2,sl).

The surface of the epidermis is frequently interrupted by hairs, and also by the openings of ordinary sudariparous and of modified sweat glands as Diem (1907), Porta (1910) and others have shown. The ordinary sweat glands and the modified sweat glands may open into the hair follicle, or independently on the surface. The distribution of skin glands over the body is very variable. Though not numerous in the region of the rump, sweat glands are, however, present. This is in accord with Diem's findings, but opposed to those of Hoffman (1898). The writer was unable to find sweat glands in the sole of the foot, and agrees with Toldt (1907) that these glands do not occur in the ball of the thumb. Toldt found numerous glands in the "Saugescheibe", and also large groups of glands in the region of the neck and of the external genitalia. The upper lip is more abundantly supplied with skin glands than any other part of the body.

As is frequently the case the superficial layer of the corium, the stratum papillare, is raised into ridges and papillae which project into the epidermis. These are most marked in the upper lip, where simple and compound papillae are present. The interlacing strands of connective tissue and the reticulum of elastic fibers which together form the ground work of the corium are comparatively fine and closely packed, thus causing this layer to be somewhat dense. Preparations stained with Mallory's connective tissue stain show that the general direction of these strands and fibers is parallel with that of the stratum Malpighii. While it is not possible to determine a boundary between the stratum papillare and the stratum reticulare, yet the deeper connective tissue bundles of the latter are obviously

more loosely interwoven than those of the superficial layer of the corium. As in other mammals, the corium contains blood vessels, hair follicles, sebaceous glands, sudariparous glands, striated and smooth muscle fibers, nerve trunks, medullated and non-medullated nerve fibers, tactile corpuscles, and nerve endings. The last three structures mentioned will be described in detail later.

The upper lip of the bat is richly supplied with skin glands. As one type of these, the modified sweat gland, differs somewhat from the typical sweat gland a description of its structure may not be out of place here. Compared with a hair follicle, this gland is enormous in size. It consists of a long, uncoiled, secreting portion with an extended funnel-shaped duct. The secretory portion is lined by a single layer of columnar cells with finely granular protoplasm and round or oval nuclei (Fig.3,cc). Leydig, Schöbl and Sabussow (1910) have called attention to the fact that these large modified sweat glands (in the flying and interfemoral membranes) have a coating of smooth muscle fibers, which by their longitudinal course cause a slight spiral striping of the gland. This coating of muscle fibers (Fig.3,mf) lies between the layer of columnar cells and an external covering or basement membrane (Fig.3,bm). The latter is homogeneous and without nuclei. The duct of the gland is lined throughout by short, somewhat irregularly cubic cells, arranged in a single layer, and surrounded by a delicate basement membrane. Not infrequently secretion products are found in the lumina of the glands. The products are more or less similar in appearance to what Wimpfheimer (1907) terms degeneration products ("detritus")

found in uncoiled sweat glands in young moles.

It is worthy of remark that pigment cells occur in the corium both of the body integument and of the flying and interfemoral membranes (Fig.2,pc). These cells are more or less similar to those pointed out by Kohn (1910) in the hypophysis of man, and closely resemble the pigmented corium tissue cells of the pia mater of sheep described by Krause (1911). In the corium of the integument they are numerous, and appear to be scattered about promiscuously. Their form is very variable. They may be spherical, oval, elongate and slightly spiral, heart-shaped, pear-shaped, raggedly lobulated, and with or without processes (Plate III, Fig.5). In size they vary from 34 micra in length and 25.5 micra in width to 374 micra in length and 60 micra in width. The cell body is filled with fine brown granules. In haematoxylin-eosin preparations a few of the granules usually take the dull blue stain of the haematoxylin, while in the methylene blue material some or all of the granules may stain a bright blue. Plate III, Fig.5,b represents a pigment cell containing stained and unstained granules.

2. Flying and Interfemoral Membranes.

The flying membrane of bats appears as a skin duplicature formed by the lateral extension of the dorsal and ventral integument of the body. The proximal parts of the membranes are covered with fine hairs similar to those of the pelage, while over the distal areas extremely fine, more or less modified hairs occur sparsely. In the natural condition there is a manifold wrink-

ling and pleating due to numerous elastic bands within the membrane (Schöbl).

Externally the flying membrane is seen to be made up of small hexagonal, plate-like cells which form a continuous membrane. Each cell contains pigment granules which are collected into an intramarginal zone much as Schöbl has described (p.4). This investigator repots that the center and border of the cell (in Vesperugo serotinus) are free from pigment granules. In Myotis lucifugus and M. sublatus the writer found pigment in both of these regions, but in smaller quantities than in the intramarginal zone. The cells of the outer (dorsal) surface of the flying membrane contain more and darker pigment granules than do those of the inner (ventral) surface (Schöbl). In fact this surface in places contains almost no pigment at all.

As in the integument of the body the epidermis of the flying membrane stands out in the sections in contrast to the cutis. The Malpighian layer also can be readily distinguished from the stratum corneum. According to Schöbl's findings the Malpighian stratum is composed of two layers of scattered cells. The writer, however, finds that one layer of cells occurs quite as frequently as two. The nuclei of the deep Malpighian layers of both dorsal and ventral sides are slightly more oval than those of the more superficial layers, the latter being somewhat flattened. From the shape of the nuclei one would infer that when a single layer occurs it is the outer one. In the Malpighian stratum of the dorsal side of the patagium numerous pigment granules are present, while in this stratum on the ventral side very little pigment occurs. Aside from being somewhat thinner,

the stratum corneum does not differ from the corresponding structure in the skin of the body.

The tissue enclosed between the dorsal and ventral Malpighian strata of the patagium constitutes the corium, which varies in thickness in different regions. In both the flying and interfemoral membranes it is thickest near the body, while in the more distal areas it gradually becomes thinner.

The corium is made up of three poorly defined strata of connective tissue--a central,somewhat loose one, corresponding to the stratum reticulare of the body integument, and two others-one on either side--of denser tissue, more or less similar to the stratum papillare. The chief arteries, which are accompanied by the larger veins and nerve trunks, cause this stratum to be much thicker in those regions where they occur than elsewhere. Although the outer surfaces of this stratum is thrown into folds to some extent, the writer has been unable to find papillae.

In the stratum reticulare are contained the larger blood vessels and nerves, and the striated muscle bundles and elastic bands (Balken) first described by Leydig, whose findings were later confirmed by Schöbl. Here also are found the secreting portions of sweat glands, and the proximal third of hair follicles. The outer stratum of the corium contains the central portions of the hair follicles, their sebaceous glands, and the sweat glands. Each follicle, with the sebaceous, sudariparous and modified sweat glands associated with it, is surrounded by a capillary network.

II.-Nerve Layers of the Integument.

1. Nerve Layers of the Body Integument.

In the sub-cutaneous tissue and in the reticular stratum of the body integument, are found large medullated nerve trunks and branches which, for convenience, are called the first nerve layer. By dichotomous branching these nerves break up into a loosely intertwined meshwork consisting of an enormous number of medullated nerves. These interwoven nerves, which are not actually united in a plexus, constitute the second nerve layer (Fig. 4,snl). Arising from the latter are medullated nerves which pass toward the periphery. Near the outer surface of the corium they begin to divide. The resulting branches pass directly to the Malpighian stratum forming the third nerve layer (Fig.4,tnl). Ordinarily so much pigment is present here that it is impossible to follow the fibrils to their endings. However, in places where the epidermis has accidently been torn, one can readily trace the fibrils well into the Malpighian stratum, noting branching fibrils which pass outward and terminate in or between the cells of the stratum granulosum. As these can be traced more readily in the membranes where little or no pigment is present they will be considered more fully later. Varicosities are numerous both in the second nerve layer and along the fibers which pass to the third layer (Figs.14,15,16,17). The greater number of these enlargements, however, occurs on the smaller fibers. Varicosities in the third nerve layer, i.e., on the surface of the corium or in the Malpighian stratum, have not as yet been observed by the

writer. As the literature on nerve layers in the skin of bats deals almost entirely with these layers in the patagium, the brief historical survey willbe given in the consideration of the flying membrane.

2. Nerve Layers in the Flying and Interfemoral Membranes.

As early as 1796 Cuvier called attention to the abundance of nerves in the flying membranes of Chiroptera. Leydig, a half-century later, while differing somewhat with Cuvier as to the number of nerves present, admitted that these membranes are richly innervated.

The first investigator, however, to make an intensive study of the arrangement of the nerves in the flying membranes was Schöbl (1871) who states that the nerves of the patagium are naturally divided into five layers. The first layer, situated in the innermost stratum of the flying membrane, contains the larger nerve trunks, the main blood vessels, the chief muscles and the elastic bands. The second nerve layer is double, one part lying above, and its duplicate below the first layer. The nerve trunks of this layer branch dichotomously again and again forming an irregular network. The third layer of nerves, which is also double, lies external to the previous one on a level with the finest blood vessels. As to the size of the nerve trunks of this layer, Schöbl states that they consist usually of two, very rarely of four non-medullated fibers. The fourth nerve layer, likewise double, lies outside of the third. It consists throughout of an irregular net of single non-medullated fibers. The

meshwork in this layer, however, arises not by an interlacing of fibers, as is the case in the other two layers, but by direct anastomosis of single non-medullated fibers. On certain fibers of this layer Schöbl noted a number of enlargements or swellings ("Krootenpunkten"), which were triangular, square, or polymorphic in form, having a fine granular appearance, but exhibiting no nuclei. He also occasionally saw more or less similar spindle-shaped enlargements in the course of a single fiber, especially the larger ones. The fifth and last nerve layer, also double, lies immediately over the previous one on the surface of the cutis, ordinarily remaining attached to the deepest cells of the Malpighian stratum. The fibers of this layer are likewise non-medullated, and have a diameter ranging from 0.9 micra to immeasurable fineness. This layer arises from the previous one by the division of the finest fibers of the latter. At the places of division of the fibers, the swellings which were found so frequently in the last nerve layer seldom occur in this one, and the spindle-shaped variety is lacking entirely. This layer of extremely fine non-medullated nerve fibrils lying immediately at the surface of the corium partly between the lowest cells of the Malpighian stratum, Schöbl holds as a terminal. He further states that in preparations in which the lowest cells of the Malpighian stratum remain undisturbed on the corium, no free endings of the finest non-medullated nerve fibrils are found, and that fibrils passing further toward the surface between the cells of the stratum granulosum, are never to be found either on the surface of the preparation or in cross section.

However, he pointed out that, occasionally, round or elliptical swollen structures resembling fine nerve endings are to be seen, but these almost always prove to be nodal points of division of nerve fibrils. These minute swellings occurred so seldom that Schöbl attributed their presence to faulty technique.

Sabussow (1910), working on the innervation of the flying membrane, did not wholly accept Schöbl's idea of the distribution of the nerves of this part of the body. This investigator found large nerve trunks in the innermost stratum of the patagium, but held that Schöbl's second nerve layer lay in the same plane as the first, and consequently could not be said to exist as a separate nerve layer. Concerning Schöbl's third layer Sabussow simply stated that it is not double. But the existence of the fourth nerve layer of Schöbl this investigator confirms, adding that no matter how the membrane is torn, this layer can be seen to be double. He also confirms Schöbl's fifth layer, which is non-medullated and double; but instead of the few"swellings" which Schöbl observed, Sabussow found numerous varicosities. The latter sums up the layers he found as follows: (1) a simple layer including the first two layers of Schöbl; (2) a broadly meshed double network with triangular enlargements in it; (3) a network of varicose fibers also double. Consequently, according to Sabussow, there are five nerve layers in the patagium.

In transverse sections of my own preparations of the flying and interfemoral membranes there can readily be seen here and there regions which are approximately twice as thick as that of the remaining area of these membranes. It is in these thickened regions that the chief arteries, veins, nerve trunks and

frequently the principal muscle bundles are found. These particular regions contain, as will be shown, one more layer of nerves than do the others.

The main blood vessels, accompanied by the chief nerve trunks, pass out from the body through the flying and interfemoral membranes in the stratum reticulare, giving off, here and there, important branches, which, as stated, are frequently found with the muscle bundles. These blood vessels, partly because of their own size, and partly on account of the increased amount of connective tissue around them, cause the elongated thickenings or ridges in these membranes already referred to. The medullated nerve trunks and their chief branches, both found in the innermost stratum (reticulare) and existing only in the aforesaid ridges, constitute the first nerve layer. The second, a double layer of nerves, arises from the first by repeated dichotomous branching, traverses the deeper part of the corium, and spreads throughout the entire area of the flying and interfemoral membranes. In methylene blue preparations this layer is seen to consist of a loose network of medullated nerve fibers, many of which contain comparatively large varicosities (Plate III,Fig.13,va). The third and last nerve layer is likewise double. Numerous medullated fibers arising from the second nerve layer pass toward the two external (dorsal and ventral) surfaces of the membranes. Many of these fibers on approaching the Malpighian stratum divide dichotomously; others do so at the surface of the corium. Both lose their medullation. The forked branching continues to some extent in the Malpighian stratum,

the larger fibrils giving smaller ones until finally delicate nerve threads are seen to end in minute enlargements, which will be described in detail later. These branchings of non-medullated nerve fibrils at the surface of the corium and in the stratum Malpighii constitute the third nerve layer. While varicosities of different sizes (Figs.13,14,15) appear in the nerve fibers leading up to this layer, the writer has not observed them in the latter.

According to the present observations, then, certain regions of the flying and interfemoral membranes are supplied with three layers of nerves, others with but two. Briefly stated their number and distribution are as follows:

1. A layer of medullated nerve trunks and numerous medullated branches, occurring in the stratum reticulare, but only in the elongated ridges containing the largest blood vessels and much connective tissue.

2. A double medullated nerve layer in the deeper part of the corium extending throughout the membranes.

3. A layer, likewise double, present in the entire Malpighian stratum, and consisting of numerous branches of non-medullated nerve fibrils.

A comparison of the foregoing findings shows that the first nerve layers of Schöbl and of the writer coincide; that Sabussow's first layer included Schöbl's first and second layers and the writer's first, together with the innermost branches of his second nerve layer. A study of sections from the different parts of the membranes has convinced the writer that Schöbl's

second, third and fourth nerve layers may well be considered as one layer, the writer's second. Close to the body, where these membranes are thick, and where Schöbl probably made his observations, since he especially recommended this region for study, it is true that the writer's second layer is thicker dorso-ventrally than it is near the elbow, or in the region midway between the body and the tail. But out at the periphery, between the elongated phalanges, and near the posterior border of the interfemoral membrane, where the skin duplicature is thin, this nerve layer is exceedingly compressed. The contention of Sabussow that Schöbl's second nerve layer lay in the same plane as the first, and consequently could not be considered as a separate layer, is not supported by the present observations. Schöbl's first layer is to be found in the stratum reticulare, while the second, arising by repeated dichotomous branching of the first, takes a position in the deeper part of the superficial layer of the corium. The writer's second nerve layer corresponds to Schöbl's second, third and fourth layers, while Sabussow's second layer includes the third and fourth layers of Schöbl, and the greater part of the writer's second. The third nerve layer of Sabussow and of the writer, respectively, correspond to Schöbl's fifth.

III.-Nerve Endings in the Integument.

The nerve terminations in the integument of Chiroptera may be grouped into five classes as follows:

1. Free nerve terminations in the epidermis.

2. Nerve endings on hairs.

3. Special sensory end-organs.

 a. End-bulbs.

 b. Terminal corpuscles.

4. Motor nerve endings on striated muscles.

5. Nerve endings on modified sweat glands.

1. Free Nerve Terminations in the Epidermis.

As was stated in an earlier part of this paper, free nerve endings in the form of minute swellings were observed in the stratum Malpighii. These free nerve terminations or end-knobs can most readily be seen in sections of the ventral portions of the membranes where little or no pigment is present. Especially desirable for this purpose are obliquely cut sections, or those which contain small areas of the surface of the membrane (Fig.6). In such sections it is possible to focus down through the transparent stratum corneum, thereby obtaining distinct views of the deeply stained (blue) nerves of the third layer (Fig.6,n). The latter stand out in bold contrast to the weakly stained cytoplasm of the Malpighian stratum. In sections 20 micra thick one can, by focusing, trace non-medullated nerve fibers, from the point of branching near the surface of the corium, on out among the deeper Malpighian cells. The larger fibrils and the smaller ones given off from them are plainly visible. Finally, among the cells of the stratum granulosum (Fig.6,sgr), the endings of the ultimate branches are seen to terminate in minute round or oval end-knobs (Figs.6,7,e). Similar structures were mentioned but

misinterpreted by Schöbl, who, on observing in the stratum Malpighii a very limited number of minute round swellings resembling fine nerve endings, concluded that they were foreign particles due to faulty technique.

The end-knobs take a deep blue stain similar to that of ordinary axis cylinders, and appear to be homogeneous in structure. As to shape they are oval or spherical. Their size varies from 0.5 micra in length and 0.4 micra in width to 0.9 micra in length and 0.8 micra in width. In the sections studied, these end-knobs appear to be numerous. Ordinarily, one to a cell is observed, though occasionally even two are seen close to a single cell boundary. It also happens sometimes that a tiny fibril appears to end without any enlargement (Fig.7,x). This, however, may be due to the failure of the methylene blue to differentiate the end-knob, as those who have worked with this stain will readily understand.

That these diminutive enlargements or end-knobs are real nerve terminations and not the nodal swellings sometimes seen where fibers divide has been satisfactorily proven. For example, in focusing on the surface of the transparent stratum corneum no knobs nor fibrils can be seen. A deeper focus brings into view end-knobs with a fine nerve fibril running into each. A still deeper focus shows tissue below the end-knobs and enables one to follow the nerve fibrils from the now indistinct terminal swellings back to the branch from which the nerve fibrils are given off. Where little or no pigment is present, these nerve terminations can be seen without difficulty.

For a time the writer was unable to determine whether the nerve end-knobs are situated in the stratum Malpighii or in the deepest layers of the stratum corneum. At length, however, a section was found in which a part of the ventral surface of the interfemoral membrane curled up permitting an oblique view. The methylene blue stain was deep enough to show the margins of a number of consecutive superficial cells of the stratum granulosum (Fig.6), and little pigment was present. By focusing upon this obliquely turned portion of the surface of the membrane, it is comparatively easy to distinguish the flat, elongate, scale-like cells constituting the stratum corneum from the more oval, clearly defined, superficial cells of the Malpighian stratum. By focusing upon the curved surface it is possible to see a number of nerve end-knobs on or near the surface of the stratum granulosum, but as yet no end-knobs have been seen by the writer in the stratum corneum.

The question of the exact position of the end-knobs in respect to the epithelial cells naturally arises. It is certain that a large number of the structures in question are situated on the surfaces of the cells (Fig.7,es). Others appear to be within the cytoplasm. However, it is frequently possible by focusing to see that these end-knobs are after all on the borders of the cells. If all were completely stained, it is not improbable that the remaining end-knobs could be shown to be intercellular.

So far as the writer has been able to ascertain the only reference to free nerve terminations in the epidermis of bats

is that of Botezat (1908). The study of this investigator was made principally on the nerves in the epidermis of the dog's nose, but he mentioned the finding of intracellular end-knobs ("Endknöpfen") in the skin of the nose of the bat. He held that the free nerve terminations in the epidermis not only of bats, but of all classes of vertebrates, are intracellular, though none of his figures indicate it. Retzius (1892) in his monumental work on the nervous system showed free nerve terminations in the epidermis of the lip of the human foetus and made the following statement: "The fine, varicose nerve fibrils branch and end intercellularly without any direct connection with the cell." He found the same to be true of the free nerve endimgs in the skin of the mouse and of the rabbit. Van Gehuchten, in 1893, described free nerve terminations in the epidermis of the face, lip, ear, paw and tail of the white mouse and white rat. He likewise found the free nerve endings to be intercellular. He stated, "Partout nous avons trouvé l' existence de fibres nerveuses intra-epidermiques se ramifiant et se terminant librement entre les cellules epitheliales." While Dogiel (1903) did not hold intracellular endings as out of the question, yet he was strongly of the opinion that the free nerve terminations are intercellular.

2. Nerve Endings on Hairs.

While the innervation of hairs has for some time been a field of fruitful investigation, there still remain some unsolved problems in connection with the hair of Chiroptera. In recent years especially, more attention has been directed toward

the innervation of tactile or sinus hairs than toward that of the hairs of the pelage. The writer's descriptions will be confined wholly to the latter.

Observations made by different investigators on the innervation of the hairs of bats have been so conflicting that it seems advisable to give a brief review of the literature. Schöbl (1871) studied the innervation of the hair of the flying membrane, and set forth the following principal points: In the hairs of the bat, the nerves terminate in special corpuscles ("Terminalkörperchen") situated at the bases of the hair follicles. The hair receives a bundle of nerves which consists of from 2 to 5 medullated fibers. These twist many times in a spiral about the hair shaft forming a nerve wreath or ring. From this spiral ring two to four nerve fibers are given off, and these extend downward ending in the terminal corpuscle beneath the hair follicle. A superficial nerve ring which consists of from one to two coils is formed by fibers from the fourth nerve layer. Boll (1871) working on similar material confirmed Schöbl's observations.

The following year Stieda took exception to Schöbl's findings, especially in regard to his "Terminalkörperchen". This observer concluded that the structure in question was not a nervous apparatus but rather a differentiated part of the hair follicle ("Haarkeime"). The nerve ring was not mentioned by Stieda.

Beil (1871) also denied the existence of Schöbl's end-corpuscles, although he was able to see the nerve ring. Concerning the structure of the latter, its course, or the endings of its fibers, he could determine nothing definitely. Above the seba-

ceous glands, however, Beil noted the entrance of two or three bundles of non-medullated nerves into the hair follicle.

Using the method described by Schöbl himself, Veleeky (1872), investigating the flying membrane, likewise did not find the so-called end-apparatus; nor did the use of gold disclose these "Terminalkörperchen". By the latter method, however, he demonstrated non-medullated nerves which approach, from below, the cells of the epithelium of the outer root sheath of the hair, and spread into the intercellular spaces, forming a net.

In the same year appeared a more important piece of work by Jobert in which he described in considerable detail the innervation of the hair in the bat's wing. The principal points brought out were as follows: (1) All the hairs of the skin are supplied with nerves and are perceptive. (2) The affirmation of Schöbl that into each hair follicle there enters one nerve is not true. Each hair is supplied with many nerve fibers, five to six or more, which approach the follicle, together or separately, and from different sides. They may unite into two or three small trunks. On reaching the neck of the hair the nerves divide, lose their medullation, and are distributed on the hyaline membrane more or less like radiations, ending freely at about the same level. (3) The nerve ring of Schöbl does not exist, neither does the "Terminalkörperchen". (4) At the level of the superficial subepithelial network of nerves, minute threads are seen which surround the follicle and disappear in the epithelial sheath.

Arnstein (1876) recognized two different kinds of nerve terminations on hairs: (1) The free endings on the hyaline membrane in the form of a "palisade". (2) The nerve network which occurs in the outer root sheath.

Bonnet (1878), who investigated the innervation of the hair follicles of a number of mammals including the bat, confirmed Arnstein's observations on the endings of nerves on the hyaline membrane. Bonnet's idea was that a nerve ring exists in connection with each hair. The small fibers which constitute this structure lie outside of the straight fibers, which terminate in a "palisade", and surround them much as hoops surround a barrel, in the form of a ring consisting of six or more pale fibers. Of the root sheaths in the region of the sebaceous glands Bonnet says, "This is a rendezvous of the various small medullated nerve fibers which come to the hair partly above and partly below the sebaceous glands. These fibers going to the follicle spread out forming a woven net of minute medullated fibers".

In describing the innervation of the hair of certain mammals including bats, Szymonowicz (1901) pointed out that the medullated fibers approach the follicle below the sebaceous glands, divide, losing their medullation, and penetrate to the hyaline membrane, where some of the fibrils encircle the hair, while others end on the hyaline membrane. The latter fibrils branch regularly, and run parallel to the long axis of the hair. This investigator observed perceptive menisci in a strongly developed outer root sheath of a common hair in the face of Ves-

perugo serotinus.

According to the observations of Sabussow (1910) the hair of the flying membrane of bats is supplied with several medullated nerve fibers whose number is never less than two. These fibers approach the hair follicle, divide, spread around the hair spirally, more or less in the form of a ring, give off small fibrils from the latter, branch, and finally end in the form of a"palisade" on the hyaline membrane. The fibrils of the "palisade" may contain varicosities along their courses, or their distal ends may be lance-shaped. The spiral ring around the "palisade" consists of small varicose threads. This Sabussow holds as a second kind of nerve ending on the hair. He asserts that he never saw these two kinds of endings, viz., the "palisade" and the varicose threads of the spiral ring, at the same time in the same hair. From this he concludes that there exist two kinds of hairs, each of which is supplied with one of these nerve terminations.

Parallel with the spiral ring just described and more superficial, Sabussow observed a broadly meshed network of fibers resembling a nerve ring, and apparently surrounding the hair above the sebaceous glands. This network or ring, which belongs to the second nerve layer, could by deeper focusing be seen to give off more or less flattened fibers resembling the "palisade". Being unable to find any definite connection between the "palisade" apparatus first described and this one which comes from the subepithelial network, Sabussow inferred that the two were independent.

In the writer's deeply stained methylene blue preparations of the bat's skin, both of the body and of the membranes, the hair follicles with their numerous nerves stand out in bold contrast to the surrounding, weakly stained connective tissue (Figs. 8,9). The nerves which supply the hairs arise from the second nerve layer, pass outward to approximately the level of the inner third of the hair follicle, where, at first, they appear to pass along from one hair to another. But upon close examination it is seen that nerves may be distributed in one of two ways: A. The whole fiber may end directly in a single follicle (Figs. 8,9,ff). B. Upon approaching hairs the nerve may divide, one or two branches going to a follicle, the others passing out to the epidermis (Figs.8,9,fe). By far the largest number of the nerves in question are distributed in the first way. The numerous fibers form a veritable network, which might justly be termed a nerve layer, but which for simplicity is not so considered by the present writer.

As to nerve endings on the hair, it may be said that they occur at three different levels and in three separate layers of the follicle. 1. A superficial nerve ring situated above the orifice of the sebaceous glands and giving off nerve threads in the connective tissue sheath (Fig.9,sn). 2. Fine varicose or flattened nerve fibrils which lie immediately below the sebaceous glands, and end on the hyaline membrane parallel to the long axis of the hair (Fig.9,eh). 3. Nerve fibrils at the level of the lower third of the follicle, which take a horizontal position in the outer root sheath (Fig.9,eo). A further consider-

ation of these types of nerve endings follow.

1. <u>Superficial nerve ring</u>.- Medullated nerve fibers approach the hair above the opening of the sebaceous glands. At the outer border of the connective tissue sheath, they divide, spreading around the follicle and forming a loose ring of from two to six or more fibers. From the ring are given off non-medullated fibrils some of which are interwoven in a delicate network, while others appear to end freely in the connective tissue sheath of the follicle. This ring doubtless corresponds to the "broadly meshed network resembling a ring" described by Sabussow (1910) above the sebaceous glands. As is seen in Figure 9,f, the non-medullated fibrils show no tendency to pass downward to a nerve ring below.

2. <u>Varicose or flattened nerve fibrils</u>.- Immediately below the sebaceous glands medullated nerve fibers, chiefly of type A. enter the region of the hair follicle, penetrate the connective tissue layers, divide, losing their myelin, and encircle the hair in a nerve ring. The number of fibers constituting the nerve ring varies from two to eight or even more. From the inside of the ring fibrils are given off which divide dichotomously. The branched fibrils assume a position parallel to the long axis of the hair, and usually end in slight enlargements (Fig.9,eh), some of which are merely small varicosities, while while others resemble the minute end-knobs seen in the free nerve terminations in the epidermis. In certain cases there are no enlargements, but in these instances the terminal fibers are flattened. This type of nerve ending undoubtedly corres-

ponds to the well known nerve ring and "palisade" described first by Arnstein (1876), and recognized since by Bonnet (1878), Szymonowicz (1901), and Sabussow (1910). Merkel (1880) described a similar end-apparatus on a common hair in the lip of a cat. The "termaisons en fourchette" of the Hoggans (1883) and the nerve rings of Retzius (1894), van Gehuchten (1896) and Ostroumow (1900) are probably corresponding nervous structures.

3. Nerve fibrils in the outer root sheath.- At the level of approximately the lower third of the root of the hair, medullated nerves penetrate the connective tissue layers of the follicle. When the hyaline membrane is reached they divide and run for a short distance onor near its surface. These nerve fibers give off a few strong non-medullated fibrils which pierce the glassy membrane, and end in the outer root sheath, usually taking a horizontal position in the latter (Fig.9,eo). The nerve endings of this type are found in a slight swelling of the root sheath, which may correspond to the superior swelling described in typical sinus hairs. So far as the writer has been able to ascertain nerve endings of this type have not previously been described in the pelage hair of the bat. While such examples are not numerous, yet they seem to him to be genuine. Nerve endings in the form of tactile corpuscles were described by Szymonowicz (1901) in the outer root sheath of a hair in the face of Vesperugo serotinus. The same observer in 1909, mentioned the finding of Merkel's corpuscles in this layer of the follicle in man. Retzius (1894) described a nerve fiber in the outer root sheath of a hair of a mouse, and Vin-

cent (1913) found nerve fibrils in this layer of the sinus hair of the rat.

3. Special Sensory End-Organs.

The literature dealing with special sensory end-organs in general has recently been reviewed by a number of investigators (Szymonowicz, 1895, Tretjakoff, 1902, Dogiel, 1903, Schäfer, 1910). Therefore only a brief survey of the observations upon such end-organs in the skin of bats will be given here.

Arnstein (1876) found in the flying membrane of a bat an end-bulb which he thought resembled the well known cylindrical end-bulb of Krause. It was possible for him to trace an axis cylinder into the organ, but he was unable to make out the ending of the fiber. In one instance, however, he saw it break up into fine fibrils. Arnstein was of the opinion that these end-bulbs occurred in the flying membrane where no hairs were present.

Schumacher, in 1907, mentioned the presence of a large number of layer-like corpuscles("Lamellenkörperchen") among the phalanges.

Sabussow (1910) investigated the flying membrane of two species of bats (Vesperugo noctula and Vespertilio Daubentonii). He stated that in weakly stained preparations he could see terminal bulbs which were divisible into two classes according to size. Some were so small that upon slight magnification it was difficult to see them; others were comparatively large, had a zigzag course, and could be recognized with ease. The latter

could also be seen in material prepared by Apathy's after-gilding gold chloride method. The general characteristics peculiar to all end-bulbs which Sabussow observed were: (1) a longitudinal course of the fibers of the enveloping connective tissue membranes, apparent in gold preparations, and (2) a delicate wavy appearance of these membranes seen in methylene blue material. The connective tissue nuclei did not stain in methylene blue preparations, but on account of the difference of refraction, Sabussow thought that by focusing he could see them. He noted that the core of the bulb was narrow, but was unable to make out its finer structure.

The consideration that led Sabussow to classify these structures under the cylindrical type of end-bulbs was chiefly the way in which the nerve fiber ended in the interior of the bulb. He observed that medullated nerve fibers divided at Ranvier's nodes, giving off several medullated branches. Ocasionally, one of these branches entered an end-bulb, and passed through the whole interior of the organ to its opposite extremity. This naked axis cylinder in the bulb became slightly expanded, and ended either with a sharp point or in a thickening resembling a button.

In his Figure 10, Sabussow pictured an end-bulb stained with methylene blue, which he called a variation of the cylindrical end-bulb type. He described it as follows: "Within the bulb the axis cylinder expands, and, in the middle, broadens into a wide, paw-like plate with deep notches in its edges. From this plate there is given off a fiber which bends backward

and upward, and in turn widens into a similar paw-like plate. The substance of the plate has a granular appearance, with here and there small masses of stain".

In my own methylene blue preparations of the integument two kinds of special sensory end-organs have been observed. (1) A small elongate end-bulb into which a single medullated nerve fiber enters, passes approximately to the opposite end, and terminates in a slight enlargement (Fig.18). (2) A large, round, cellular corpuscle innervated by a single fiber which disappears among the cells of the organ (Figs.19,20). A more detailed description of each type follows.

a. <u>End-bulbs</u>.- These structures occur in the corium near hair follicles, but clearly outside of the root sheaths. Ordinarily they are found below the level of the sebaceous glands parallel with the long axis of the hair. Their size is approximately 1.5 micra in length by 0.5 micra in width. In general appearance they are regularly club-shaped in outline, the interior being filled with a semi-fluid substance. The medullated nerve, on entering the bulb, loses its myelin, the sheath of which becomes continuous with the sheath of the end-bulb. After passing through half the length of the organ, the axis cylinder expands slightly into a flat plate (Fig.18,p) which gives off two or three short heavy branches, and terminates near the end of the bulb in a small enlargement (Fig.18,en). The deeply stained blue plate stands out in bold contrast to the weakly colored bulb about it. The distal branch arising from the thickened axis cylinder usually bends to one side, breaks up into an irreg-

ular, elongate, granular mass, and as such extends back through the expanded part of the bulb (Fig.18,br). In the portions of the organ surrounding the plate and the recurrent granular mass no layers nor nuclei are visible. With the exception of the lack of nuclei the appearance of this end-bulb is practically identical with that of the structure which Sabussow (1910) showed in his Figure 10, and which he termed a modified end-bulb of Krause. The absence in my preparations of the nucleated capsule characteristic of the cylindrical end-bulb of Krause can be explained by the fact that such structures do not ordinarily stain in methylene blue. Although these organs are somewhat smaller than the cylnidrical end-bulbs in question, their location and structure are such that the writer is inclined to think that they are modified cylindrical end-bulbs of Krause.

b. Terminal corpuscles.- These conparatively large spheroidal corpuscles are found in the stratum reticulare of the corium, usually at some distance beneath the lower level of the hair follicles. In methylene blue preparations they stain deeply, exhibiting a cellular appearance, and frequently showing one or more nuclei (Figs.19,20). Their size, which is fairly constant, is approximately 20 micra in length by 10 micra in width. Each corpuscle is innervated by a medullated fiber which arises from the second nerve layer. The fiber passes into the deeper part of the corium, and after giving off a few branches enters the corpuscle, where it disappears among the cells. Occasionally, the fiber, on approaching the organ in question, forms a slight spiral coil (Fig.19). Thus far it has been impossible to trace

the course of the nerve fiber within the corpuscle. To establish the identity of these organs with any of the known types of corpuscles is difficult. The layer-like capsules characteristic of Pacinian corpuscles are not apparent, but their absence may be due to incomplete staining. They more nearly approach the size of the type in question than that of any other type of corpuscles commonly found in the mammalian skin. Their location is identical with that of Pacinian corpuscles. From the facts set forth it seems possible that these spheroidal, cellular bodies may be Pacinian corpuscles.

To these two types of sensory end-organs may be added terminal varicosities, which are abundant in the region of hair follicles, outside of the root sheaths. Comparatively strong nerve fibers can be seen to enter these structures, where they break up into fine fibrils, and are surrounded by neuroplasm. It is possible that these organs are varicosities in which the fibers beyond the enlargements fail to stain. But they are found constantly in deeply colored preparations, and moreover, are somewhat greater in size than those ordinarily occurring in the course of a fiber. Arnstein (1876) described varicosities in the outer root sheath of sinus hairs in bats, and Sabussow mentioned the presence of these structures on the courses of nerves outside of the root sheaths, but it appears that terminal varicosities external to the hair follicles have not previously been observed in Chiroptera.

Remarks on Sabussow's second type of end-bulb.- As has been shown the writer confirms one type of Sabussow's end-bulbs, the

first, which closely resembles Krause's cylindrical end-bulb (Fig.18, Sabussow's Fig.10). But the Russian author's second type, viz., the large one containing a nucleated sheath, and having a zigzag course, has not yet been seen in the preparations used for this study. However, there are present in this material structures (portions of medullated nerve trunks) which correspond so closely to the descriptions and pictures of his second type of end-bulb (Sabussow's Plate I,Fig.5,6,7,8,9) that it appears very probable that the two are identical. In his Figure 8, he shows "end-bulbs", which to the writer, seem clear examples of cut medullated fibers separating out from a common trunk. Sabussow, himself, points out that medullated fibers in this region branch repeatedly at the nodes of Ranvier. His Figure 7, a picture of two so-called end-bulbs, is apparently a portion of a medullated nerve fiber, which at one of these nodes, divides into branches. In his descriptions he states that the axis cylinder passes through the whole bulb to its very end. This is precisely what is found in a portion of a medullated nerve (Fig.21) when cut obliquely. The "ending" of the axis cylinder appears pointed or hooked according to the position of the nerve when cut. The connective tissue nuclei, which did not stain in methylene blue, but which Sabussow thought he could make out by focusing, are in the opinion of the writer nuclei of the sheaths of Schwann or of the perineurium.

In the present investigation no gold chloride method was used, but material prepared by the Cajal silver nitrate method, Bielschowsky's method, and with methylene blue counter-stained

with carmalum, has failed so far to reveal the presence of this second type of "end-bulb" as described by Sabussow.

4. Motor Nerve Endings on Striated Muscles.

Voluntary muscles in the integument of the face, especially in the upper lips of bats, are well developed. In sections stained intra vitam with methylene blue these muscles are ordinarily deeply colored, the cross striations being of a slightly darker hue. Under such conditions it is usually possible to make out only the muscle fibers and their nuclei; but in regions somewhat removed from the larger blood vessels, where the blue stain is weak, one can see medullated nerve trunks among the muscle bundles. Along the muscle fibers which are stained only sufficiently to see their outline, it is possible to trace medullated nerve fibers (Fig.11,nv) which give off a small number of branches The latter in terminating form motor end-plates (Figs. 11,12, mep) on the muscle fibers.

It is not the purpose of the writer to enter into a discussion of the literature on this important subject, but merely to describe his observations and to mention wherein they agree or disagree with the findings of a few recent workers. For a review of the literature on motor nerve endings see Boeke (1909), Dogiel (1906), Huber and DeWitt (1897).

As a rule the medullated nerve fibers can be traced to the border of the muscle fiber. At, or near the edge of the latter the medullation stops, and the nerve fibers soon begin to separate into their component fibrillae, and finally end in a more

or less regular end-net or arborization (Figs.11,12,ea). This is in accord with the observations of a number of investigators including Boeke, who described motor end-plates on muscles in the tongue of the bat.

At the point where the nerve fibers enter the enlarged motor end-plate there is a slight elevation of the surface of the muscle(Fig. 12,el). The position of end-plates on muscle fibers has been in doubt for some time. In the preparations used in this study they appear to be beneath the sarcolemma (fig.11,sa). This shows especially well in cross sections of muscle fibers in the tongue (Fig.12,sa). Most investigators are now in accord in regarding this structure as under the sarcolemma.

In weakly stained preparations the branched endings can be seen to lie in more or less irregularly shaped matrices. The latter are of two kinds: (1) A weakly stained area containing numerous deeply colored granules of various sizes. (2) A somewhat smaller area without granules.

In shape, the former are irregularly circular or even triangular. The granules, which vary greatly in size, stain almost if not quite as deeply as the nerve fibrils themselves (Fig.11, mag). To structures corresponding to these Kühne (1887) gave the name soles ("Sohlen"). The smaller areas or soles, which appear to be free from granules in this stain, are oval or pear-shaped, the axis cylinders always entering the narrowed end. Huber and DeWitt (1897), Dogiel (1890) and Retzius (1892) stated that the sole does not stain in methylene blue preparations, whether examined at once or fixed in ammonium molybdate and

studied in sections. The material, from which the present observations were made, was prepared according to the latter method. The irregularly shaped matrix in which the axis cylinder terminates is typically granular, but the nuclei, seen by Huber and others in such preparations countered with carmalum or picrocarmine, do not stain with methylene blue. In each of the two matrices or soles described above, the end-arborizations are nearly similar. The fact that Huber and the other observers mentioned failed to see soles whose granules stained in methylene blue preparations, may have been due to the inconsistency of the stain. This possibility, together with the fact that nerve terminations in the motor plates are very similar in each kind of sole described, and that the size of the so-called second kind comes within the possible range of that of the first, leads the writer to think that perhaps the apparently different kinds of soles found by him in the striated muscles in the epidermis of the bat are in reality one and the same type. In the one, the granules have stained, in the other they have not.

5. Nerve Endings on Modified Sweat Glands.

So far as the writer has been able to ascertain, the literature contains no reference to the innervation of sweat glands in bats. As was noted elsewhere, the modified sweat glands (Fig. 10) have a coating of smooth muscle fibers which are arranged longitudinally (Fig.10,mu). In a weakly stained methylene blue preparation from the interfemoral membrane of a bat (Myotis lucifugus), such sweat glands have been observed with numerous

stripes running at right angles to the smooth muscle fibers (Fig. 10,fi). These stripes, which occur at comparatively regular intervals, extend hoop-like around the secretory portion of the gland external to the muscle fibers. The structures in question are much smaller than the muscle fibers, have a wavy course, and take the deep blue stain characteristic of nerve fibrils. A number (2 to 5) of delicate non-medullated nerve fibers (Fig.10,no) can be traced to the sides of these glands, but whether they connect with these circular stripes, the writer is at present unable to ascertain.

That sweat glands are under the control of the sympathetic nervous system is generally recognized. As is well known, preganglionic neurites leave the spinal cord through the ventral roots of the spinal nerves, and, after a shorter or longer course, terminate in some sympathetic ganglion in a very characteristic manner. Here the pre-ganglionic neurites branch repeatedly, dividing into numerous small varicose nerve fibers, which interlace to form intracapsular plexuses around the cell bodies of the sympathetic neurones. It is likewise well known that in the sympathetic ganglia of Mammalia such intracapsular pericellular plexuses may be very simple, consisting of only a few varicose fibrils, as well as very complex. The general structure of these pericellular plexuses, the absence of definite observations upon endings of sympathetic neurites (post-ganglionic) on sweat glands, and the striking hoop-like arrangement of these fibrillar stripes around the glands, lead the writer to question whether, perhaps, the post-ganglionic neurites may not form simple plexuses about

the glands more or less similar to the pericellular plexuses about the cell bodies of the sympathetic neurones. Such an arrangement of the terminal fibers of a post-ganglionic neurite would be most effective. The nerve threads lying immediately upon the smooth muscle fibers and on the bases of the gland cells could form functional connections with them. This view of the endings of post-ganglionic neurites on modified sweat glands seems somewhat more plausible from the fact that these circular fibrillar structures appear about the glands only on their secretory portions, and likewise only in the regions covered by the longitudinal smooth muscle fibers.

IV.-What Sensory Organs are Concerned when Blinded Bats Avoid Obstacles while on the Wing ?

Although the present problem is primarily a morphological one, yet the functions of the integumentary sense organs here described is a closely allied subject. Of especial interest is the question of the means by which blinded bats avoid obstacles while on the wing. The problem is manifestly a difficult one. A number of explanations have been offered, the more important of which are mentioned below.

Jurin (1798), experimenting upon living bats, observed that when their organs of hearing were destroyed, they were unable to avoid the obstacles placed in their way. A mutilation so severe as this, however, would certainly produce shock effects which might affect very considerably the results of the experiments.

Jobert (1872), who thought that the epidermis of bats is not especially sensitive, observed that on pinching the skin, the animals responded faintly as compared with their vigorous reactions when hairs were pulled out. This led him to think that the sensitiveness of the flying membrane is due to the hairs. He inferred that currents of air affect the hairs and that each movement of the latter is transferred to the nerve ring in such a way that objects are perceived and avoided.

Redtel (1873) also was of the opinion that the moving bat sets up air currents between itself and the object and that these stimulate sensory organs in the wings.

Rollinat and Trouessart (1900) attributed this capacity for avoiding objects to a sixth sense, that of direction.

Hahn (1908) agreed with Jurin that objects are perceived by flying bats chiefly through sense organs located in the internal ear. He closed the external auditory meatus with plaster of Paris and found that the percentage of "hits" was much higher for this experiment than for any of the others. The fact should not be overlooked that the placing of a hard substance like the one used in the meatus and possibly against the sensitive tympanic membrane is likely to interfere seriously with the normal functioning of the nervous system.

Sabussow (1910), like Jobert, was of the opinion that air currents were set up between the object and the approaching blinded animal, and that by means of these currents the nerves of the hairs were affected.

It is thus seen that the weight of evidence favors the view

that condensations (pressures) of the atmosphere set up between the obstacle and the blinded bat stimulate sensory structures in the integument.

The question of what organs are concerned naturally arises. Organs capable of being stimulated by such condensations would have to meet certain requirements. (1) They must be distributed over the head and flying membranes at least, as these parts are foremost in flight. (2) They must be superficially located, for stimulations from air condensations are doubtless very slight.

While no special nerve structures that appear to form the sole basis for the perception of air pressures have been observed by me, yet the presence of large numbers of free nerve terminations (end-knobs) near the surface of the epidermis seems significant. These structures comply with both of the requirements set forth. They are widely distributed over the body and membranes, and their superficial position among the outermost cells of the stratum Malpighii makes them especially well placed for the reception of light touch stimuli. Their number in the epidermis is enormous.

The superficial nerve rings (and their terminal fibers), though not located as near the surface of the integument as the nerve end-knobs, are so situated about the necks of the follicles as to be affected by even the slightest movements of the hairs. These nervous structures are also widely distributed over the skin and their position is somewhat superficial. Von Frey (1894-95-96), in his researches on the sense of pressure in man, has shown that pressure nerve fibrils terminate in a ring surrounding the hair follicle, this form of termination serving as an

end-organ. This writer states that on account of the position of the ring, the fibrils are stimulated by any pressure exerted upon the hair. The other nerve endings on hairs of bats are farther from the surface, so that movements of the hair sufficient to stimulate them would probably have to be more pronounced than those produced by condensations of the atmosphere.

An examination of the anatomical evidence thus indicates that two types of sensory end-organs in the skin of Chiroptera meet the requirements mentioned for the perception of air pressures. These are the free nerve terminations, and the superficial nerve rings of hairs.

End-bulbs and terminal corpuscles no doubt are tactile in function, but their depth below the surface of the epidermis precludes any probability that they aid in the perception of condensation pressures of the air.

As no sensory nerve endings on muscle fibers have been observed in this study they will not be discussed here.

As to which of the two sensory endings mentioned above function to the greater extent in the perception of atmospheric pressures, it should be pointed out that the area of the integument supplied by superficial nerve rings is insignificant in comparison with the area supplied with nerve end-knobs. Likewise, the number of terminal fibers of the rings is not to be compared with the enormous number of end-knobs in the epidermis.

As is well known the human cornea is very sensitive to delicate tactile stimuli. Conheim (1867) has shown that the only type of perceptor to be found in the cornea is that of free

nerve terminations.

Goldscheider, in 1886, determined by experimentation the location of tactile spots on his arm, and then removed for study pieces of skin containing them. Here, also, the only sensory structures revealed by a histological examination were free nerve terminations.

It, of course, is not to be inferred that all of the free end-knobs function alone as pressure perceptors, for, as is well known, the sensory nerves of the human skin mediate at least four different qualities of sensations, viz., pressure, warmth cold and pain. But the number of nerve end-knobs in the skin is so great, and the latter in the bat is so sensitive to delicate tactile stimuli, that the number of free nerve terminations in the epidermis functioning as pressure perceptors must necessarily be very large.

To sum up,then, the writer is of the opinion that the most reasonable explanation of the avoidance of obstacles by blinded bats involves the assumption that condensations of the atmosphere are set up between the obstacle and the approaching bat, and that these condensations are perceived by the blinded animals chiefly by means of the free nerve end-knobs in the epidermis, but also in part by the superficial nerve rings of the hair follicles. Such sensory impulses could be transmitted to the central nervous system, and motor ones be carried back to the muscles of the wings, in ample time for the bats to avoid the obstacles. Their tolerably slow, zigzag flight is in itself an adaptation for this purpose. From the fact that certain senses in

lower animals are developed to a higher degree than corresponding ones in man, e.g., smell in dogs, sight in birds, and from the anatomical and experimental evidence at hand, it seems very possible that the integument of bats has become far more sensitive to touch stimuli than the human skin.

SUMMARY.

I.-General Structure of the Integument.

1. The integument of Chiroptera has a general covering of hair, although the soles of the feet, the mammae, the external genitalia, and the distal parts of the ears and of the flying and interfemoral membranes are almost naked.

2. The skin consists of epidermis and corium. The epidermis is made up of a well developed stratum corneum (whose deepest layers, the stratum lucidum, can be seen distinctly only in the palmar and plantar regions) and of a Malpighian stratum. In the integument of the body the Malpighian stratum contains the three layers commonly found in the mammalian skin, while this stratum in the membranes consists at most of but two layers, and frequently of but one. The corium is composed of an external stratum papillare, containing both simple and compound papillae, and of an internal stratum reticulare.

3. Pigment granules are abundant in the Malpighian stratum, while in the stratum corneum they are much less numerous. In the flying and interfemoral membranes more pigment is present in the dorsal than in the ventral duplicature of the epidermis. Isolat-

ed pigment cells are of frequent occurrence throughout the corium.

II.-Nerve Layers of the Integument.

1. In the integument and subcutis of the body three layers of nerves are found. The first (most internal) layer consists of medullated trunks in the subcutaneous tissue. By dichotomous branching these nerves break up into a loosely intertwined meshwork consisting of an enormous number of medullated nerves, and forming the second nerve layer. Arising from the latter are medullated fibers which pass to the stratum Malpighii. Here they divide, forming a simple network, which constitutes the third nerve layer.

2. Certain regions of the flying and interfemoral membranes have three layers of nerves, others but two. These are (1) a layer of medullated nerve trunks with numerous medullated branches, occurring in the stratum reticulare, but only in the elongated ridges containing the largest blood vessels and much connective tissue; (2) a double, medullated nerve layer in the deeper part of the corium extending throughout the membranes; (3) a layer, likewise double, present in the entire Malpighian stratum, and consisting of a large number of branching non-medullated nerve fibrils.

3. Numerous varicosities are found in the corium on branches from the second nerve layer.

III.-Nerve Endings in the Integument.

1. Free nerve terminations occur in the Malpighian layer. Small medullated fibers from the third nerve layer can be traced out among the deeper Malpighian cells to the stratum granulosum, where they terminate in minute end-knobs probably intercellularly.

2. Nerve fibers supplying the hair follicles may be distributed in two ways. (a) The whole fiber may end directly in a single follicle. (b) On approaching hairs a fiber may divide, one or two branches going to a follicle and the others passing out to the epidermis.

3. Nerves end on pelage hairs at three levels and in three different sheaths of the follicles. These endings are: 1. A superficial nerve ring situated above the orifice of the sebaceous glands, and giving off nerve threads in the connective tissue sheath. 2. Fine varicose or flattened nerve fibrils which lie immediately below the sebaceous glands, and terminate on the hyaline membrane parallel to the long axis of the hair. 3. Nerve fibrils at the level of the lower third of the follicle, which take a horizontal position in the outer root sheath.

4. Two types of special sensory end-organs are found in the skin. 1. A small elongate <u>end-bulb</u> into which a single medullated nerve fiber enters, passes approximately to the opposite end, and terminates in a slight enlargement. 2. A large, round, cellular <u>terminal corpuscle</u> innervated by a single fiber whose branches disappear among the cells of the organ.

5. Terminal varicosities are abundant in the region of the

hairs outside of the sheaths of the follicles.

6. In the skin of the face, especially, striated muscles are well developed. Motor end-plates occur on these muscles. In the integument the end-plates appear to be beneath the sarcolemma, and in the muscles of the tongue these plates are clearly below the sarcolemma.

7. Small fibers resembling sympathetic post-ganglionic neurites extend hoop-like around the large modified sweat glands external to the longitudinally arranged smooth muscle fibers.

8. Blinded bats when on the wing probably perceive obstacles through the sense of touch by the effect of condensations of the atmosphere (produced on approaching the object) upon the free nerve terminations in the epidermis and the superficial nerve rings of the hair follicles.

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EXPLANATION OF FIGURES.

All figures are from bat integument except Figure 12, which is from bat's tongue. All, with the exception of Figures 2 and 3, were drawn with the aid of the camera lucida. Figures 2 and 3 were drawn with the aid of the Spencer projection apparatus. The magnifications follow the descriptions of the figures.

Abbreviations.

a ......Pigment cell with granules stained.

ax .....Axis cylinder.

b ......Pigment cell containing both stained and unstained granules.

bm .....Basement membrane.

br .....Distal branch of axis cylinder.

c ......Pigment cell with granules stained.

cc .....Columnar cells.

co .....Corium.

cs .....Connective sheath.

e ......End-knob (free nerve termination).

ea .....End arborization.

eh .....Nerve endings on hyaline membrane.

el .....Elevation where axis cylinder pierces the sarcolemma.

en .....Enlarged ending of axis cylinder.

eo .....Nerve endings in outer root sheath.

ep .....Epidermis.

es .....End-knob on surface of cell.

f ......Fibrils from superficial nerve ring.

fe .....Nerve fiber giving one branch to hair follicle and another to epidermis.

ff .....Whole fiber ending in single follicle.

fi .....Hoop-like fibril on modified sweat gland.

h ......Hyaline membrane.

hf .....Hair follicle.

hs .....Hair shaft.

ma .....Matrix of motor end-plate without granules.

mag ....Matrix of motor end-plate with granules.

mal ....Stratum Malpighii.

mep ....Motor end-plate.

mf .....Smooth muscle fiber.

mn .....Nucleus of smooth muscle fiber.

mu .....Striated muscle fiber.

n ......Nerve of third layer.

no .....Non-medullated nerve.

nu .....Nucleus.

nv .....Motor nerve fiber.

o ......Outer root sheath.

p ......Plate (expanded axis cylinder).

pc .....Pigment cell.

pg .....Pigment granules.

sa .....Sarcolemma.

sc .....Stratum corneum.

sgl ....Sebaceous gland.

sgr ....Stratum granulosum.

sl .....Stratum lucidum.

sn .....Superficial nerve ring.

snl ....Second nerve layer.

tnl ....Third nerve layer.

va .....Varicosity.

x ......Terminal fiber without bulb.

Fig. 1. Part of a transverse section of the skin of the face. pg Pigment granules. mal Stratum Malpifgii. sc Stratum corneum. Fixed in corrosive-acetic, and stained in haematoxylin and eosim. X 200.

Fig. 2. Portion of transverse section of integument at base of thumb. co Corium. mal Stratum Malpighii. pc Pigment cell. sc Stratum corneum. sl Stratum lucidum. Fixed in corrosive-acetic, and stained in haematoxylin and eosin. X 300.

Fig. 3. Transverse section of modified sweat gland from wing membrane. bm Basement membrane. cc Columnar cells. mf Smooth muscle fibers. mn Nucleus of smooth muscle fiber. Stained intra vitam with methylene blue, fixed in ammonium molybdate, and counter-stained with Mayer's carmalum. X 900.

Fig. 4. Part of a transverse section of skin of face. ep Epidermis. hf Hair follicle. sgl Sebaceous gland. snl Second nerve layer. tnl Third nerve layer. Stained intra vitam with methylene blue, and fixed in ammonium molybdate. X 450.

Fig. 5. Pigment cells in the corium of skin of face. a Cell with granules unstained. b cell containing both stained and un-

Figs. 6,7. Portions of epidermis of interfemoral membrane. e End-knob (free nerve termination). es End-knob on surface of cell. n Nerve of third layer. sgr Cell of stratum granulosum. x Terminal fiber without end-knob. Stained intra vitam with methylene blue, and fixed in ammonium molybdate. X 700.

Fig. 8. Portion of transverse section of skin of back. ep Epidermis. fe Nerve fiber giving one branch to hair follicle and one to epidermis. ff Whole fiber ending in hair follicle. Stained intra vitam with methylene blue, and fixed in ammonium molybdate. X 200.

Fig. 9. Longitudinal section of hair follicle. Drawn from a methylene blue preparation, but some features of the hair sheaths have been added from other preparations. cs Connective tissue sheath. eh Nerve endings on hyaline membrane. eo Nerve endings in outer root sheath. f Fibrils from the superficial nerve ring. fe Nerve fiber giving one branch to hair follicle and one to epidermis. ff Whole fiber ending in single follicle. h Hyaline membrane. hs Hair shaft. o Outer root sheath. sgl Sebaceous gland. sn Superficial nerve ring. Stained intra vitam with methylene blue, and fixed in ammonium molybdate. Other features from preparations fixed in Zenker's fluid, and stained in haematoxylin and eosin. X 900.

Fig. 10. Portion of modified sweat gland from interfemoral membrane. fi Hoop-like fibril resembling sympathetic nerve fibril. mu Smooth muscle fiber. no Non-medullated nerve. Stained intra vitam with methylene blue, and fixed in ammonium molybdate. X 700.

Fig.11. Striated muscle from upper lip. ea End arborization.

mag Matrix of motor end-plate. mu Striated muscle fiber. nu Nucleus. nv Motor nerve fiber. Sa Sarcolemma. Stained intra vitam with methylene blue, and fixed in ammonium molybdate. X 1800.

Fig. 12. Transverse sections of striated muscles of tongue. ea End arborization. el Elevation where axis cylinder pierces the sarcolemma. ma Matrix of motor end-plate without granules. mep Motor end-plate. sa Sarcolemma. Stained intra vitam with methylene blue, and fixed in ammonium molybdate. X 1800.

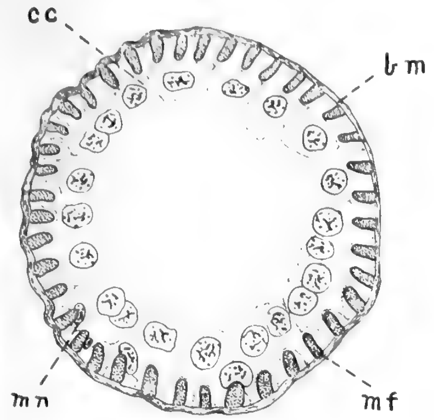
Fig. 13. Portion of transverse section of wing membrane showing varicosity on fiber terminating in epidermis. mal Stratum Malpighii. sc Stratum corneum. va Varicosity. Stained intra vitam with methylene blue, and fixed in ammonium molybdate. X 1800.

Figs. 14,15,16,17. Varicosities on nerve fibers in skin of face. Stained intra vitam with methylene blue, and fixed in ammonium molybdate. X 1800.

Fig. 18. End-bulb from upper lip. br Distal branch of axis cylinder. en Enlarged ending of axis cylinder. p Plate (expanded axis cylinder). Stained intra vitam with methylene blue, and fixed in ammonium molybdate. X 1800.

Figs. 19,20. Terminal corpuscles in skin of back. nu Nucleus. Stained intra vitam with methylene blue, and fixed in ammonium molybdate. X 900.

Fig. 21. Section of nerve trunk from interfemoral membrane. ax Axis cylinder. Stained intra vitam with methylene blue, and fixed in ammonium molybdate. X 200.



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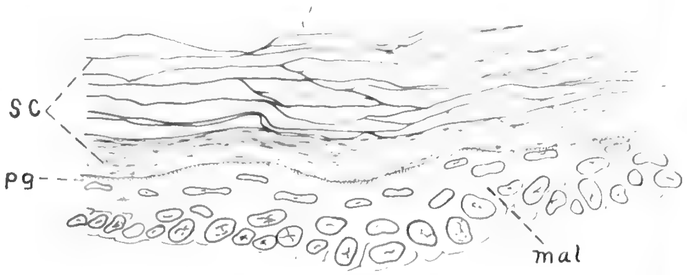

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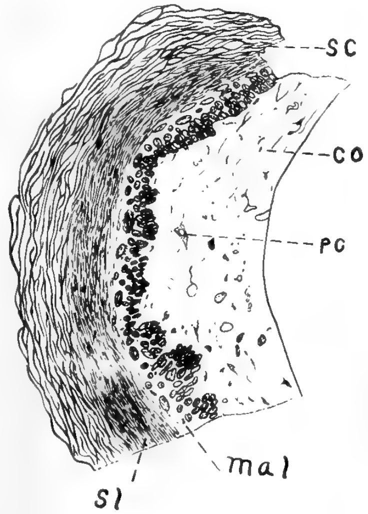

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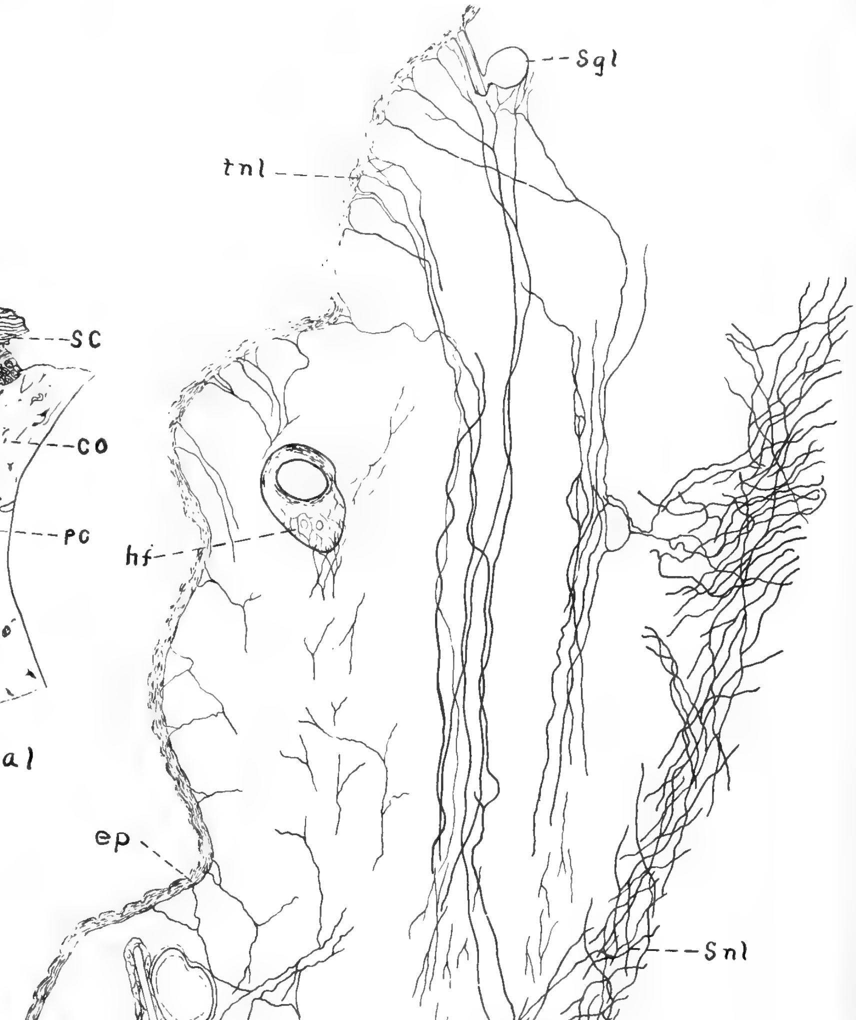

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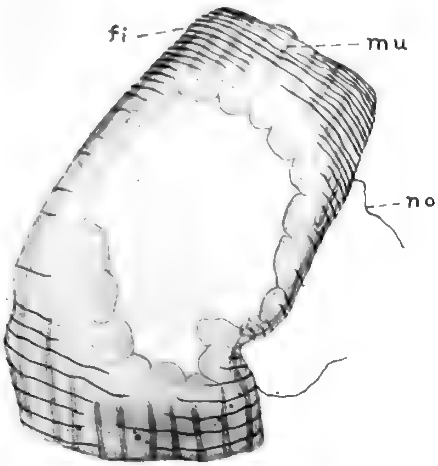

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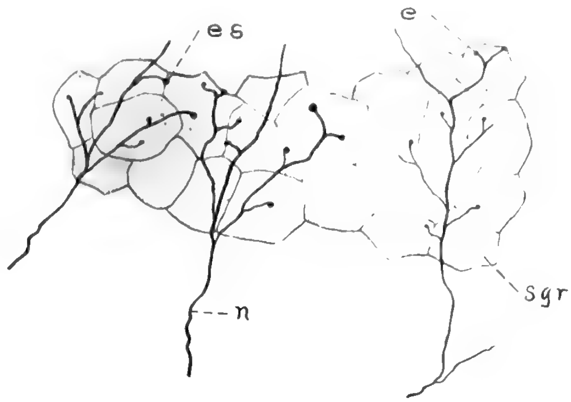

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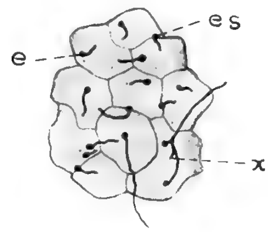

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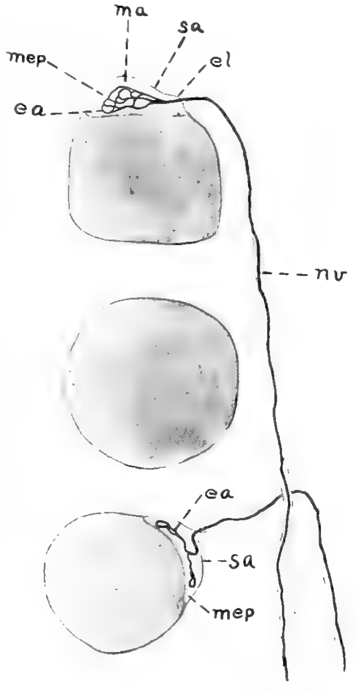

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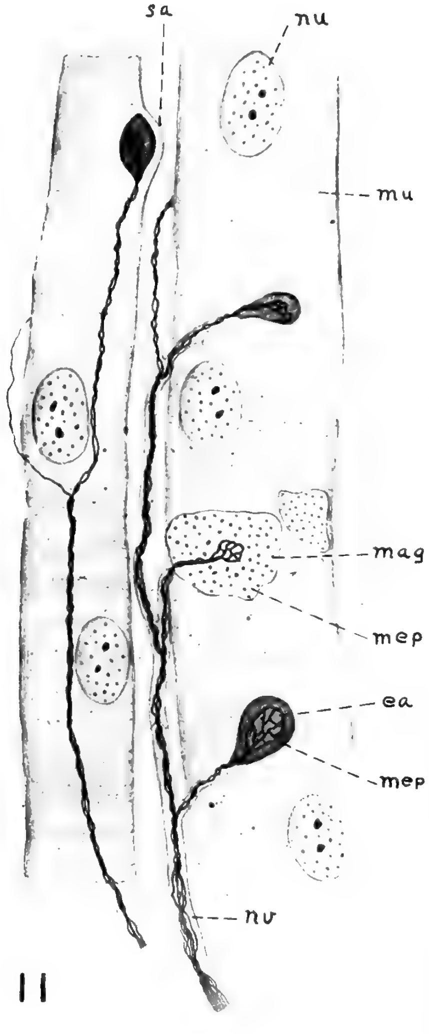

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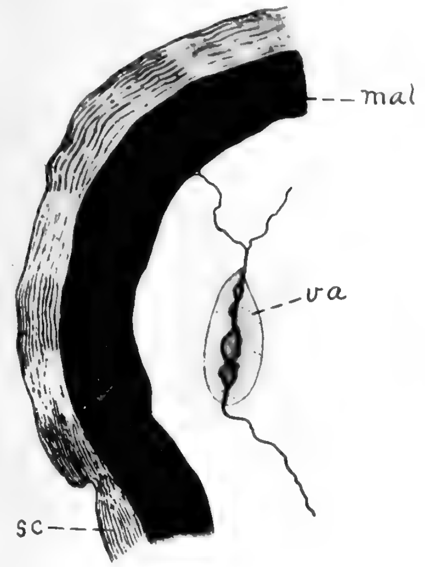

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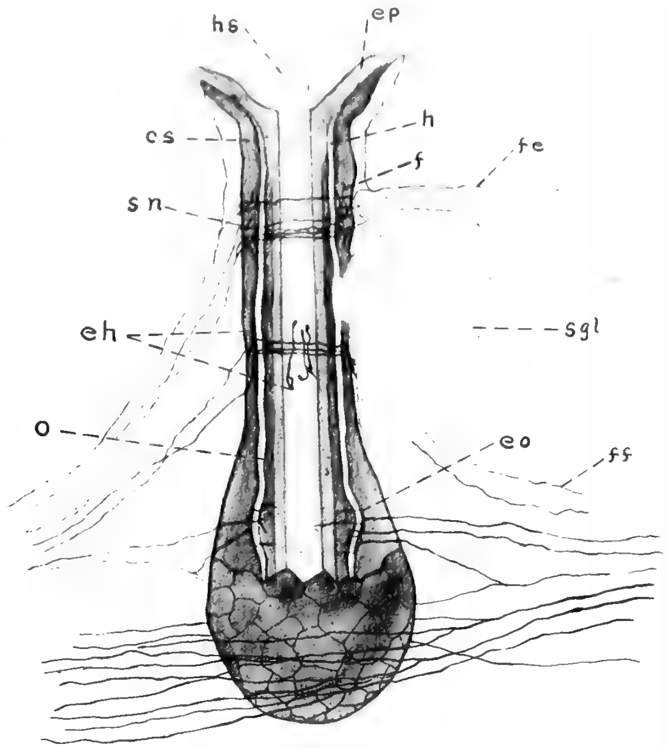

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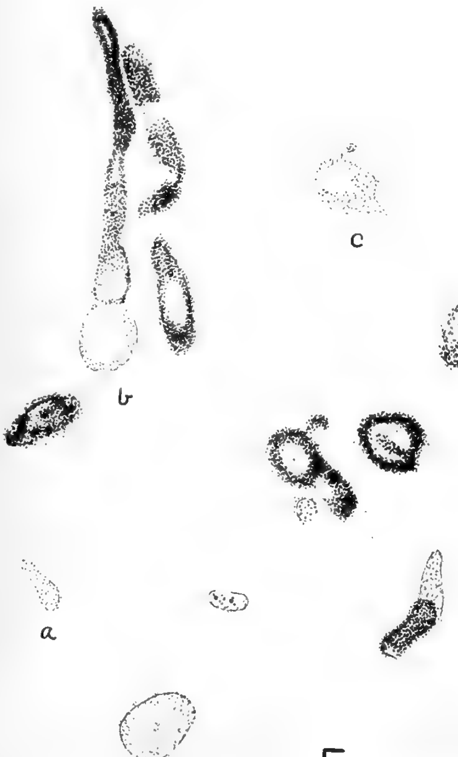

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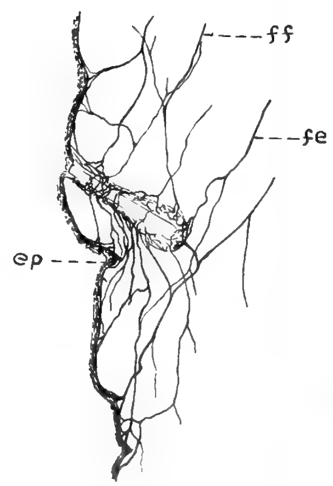

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Plate IV.

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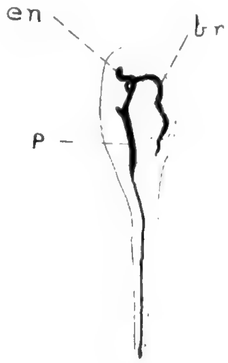

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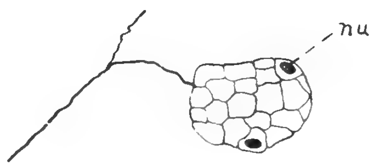

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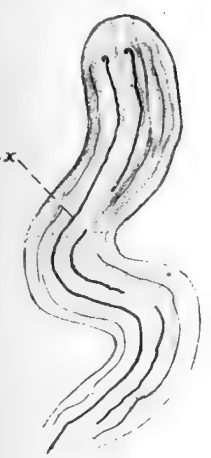

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VITA.

The writer was born August 31, 1879, at Woosung, Illinois. He received his elementary education in country schools in the vicinity of Dixon, Illinois. After teaching two years in a similar school, he attended the Northern Illinois State Normal School, Dekalb, Illinois, completing the three-year course in this institution in June, 1903. The four succeeding years he was principal of the Algonquin (Ill.) High School where he taught zoology, entomology and physiology. In 1907 the writer entered the University of Illinois, Urbana, Illinois, registering in the General Science course and majoring in zoology. Two years later he was graduated from this institution, with the degree of bachelor of arts. The two years following (1909-1911) he pursued graduate work in zoology at Illinois, serving at the same time as graduate assistant in this subject, and received the degree of master of arts at the end of this period. During the years of 1911-1912 and 1912-1913, while continuing his graduate work on a fellowship, he investigated a problem in connection with the Vertebrate nervous system.

In the last few years the writer has taken a six weeks' course at the University of Illinois Biological Station, Havana, Illinois; spent three weeks at the Biological Station of the University of Colorado, Tolland, Colorado, taking notes on the fauna and flora of the region; and worked six weeks at the San Diego Marine Biological Station, La Jolla, California, collecting and identifying specimens. The writer is a member of the fol-

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